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A PRELIMINARY STUDY OF THE SILURIAN CERATIOCARIDIDS (CRUSTACEA: PHYLLOCARIDA) OF LESMAHAGOW, SCOTLAND

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The following ten species of *Ceratiocaris* have been recorded by Peach (1901, pp. 450-451) and Jones and Woodward (1888b, p. 72) from beds of uppermost Valentian age in the Lesmahagow inlier, Lanarkshire, Scotland:

C. inornata M'Coy, 1851
**C. angusta* Etheridge, Woodward and Jones, 1886b
**C. laxa* Etheridge, Woodward and Jones, 1886b
C. longa Jones and Woodward, 1885
C. murchisoni (Agassiz), 1837
**C. papilio* Salter, 1859
**C. stygia* Salter, 1860
C. patula Etheridge, Woodward and Jones, 1888
C. robusta Salter, 1860
C. attenuata Etheridge, Woodward and Jones, 1886b
[=*C. tyrannus* Salter *in* Etheridge and Newton, 1878, *nom. nud.*]

Species indicated by an asterisk are based on type specimens from Lesmahagow. It is unlikely that ten sympatric species of *Ceratiocaris* would be ecologically compatible (Gause's principle — see also Simpson, 1961, p. 74), and examination of the supposedly diagnostic characters of these species suggests that the majority are mere variants. Thus *C. inornata* is stated by Jones and Woodward (1885, p. 394; 1886a, p. 343; 1888b, p. 37) to "agree perfectly in form and proportions [of the carapace] with *C. papilio* from Lesmahago, also in ornament, except that the postero-dorsal convergence of the striae is not present." Yet elsewhere they state that the *C. inornata* from Lesmahagow (BM 59648) is "near to *C. papilio* in form" but that its "proportions are different from those of *C. papilio*" (1885, pp. 460-461; 1886a, p. 346; 1888b, p. 49). My own measurements (W.D.I.R.) on this specimen differ from those given by Jones and Woodward, but even if their values are taken the proportions are found to be identical with the figured specimen of *C. papilio* provided by Jones and Woodward (1885, pl. 10, fig. 1; 1888b, pl. 12, fig. 1). The specimen is too poorly preserved to distinguish whether the diagnostic striae convergence is present or not.

C. laxa is a juvenile instar of *C. papilio,* as Jones and Woodward first thought (1885, p. 396). *C. murchisoni* is used to denote moderately large styles of several species, in this case of *C. papilio.* In Etheridge, Jones and Woodward's own words "*C. robusta,* being based on some small caudal appendages without carapaces, is troublesome and unsatisfactory to deal with. We find some equivalent styles and . . . stylets in *C. papilio, stygia, acuminata* etc., but none of these seem small enough for the several little sets of trifid appendages, more or less perfect, which we have met with. *C. robusta* takes in some of these; but Oxford Mus. T is relatively broad, and might be termed *lata* [= *patula* 1888]; BM 58878 from Muirkirk has very narrow members (*angusta*)." *C. longa* was first regarded as a variety of *C. robusta* (1885, p. 464) although some specimens "may well belong to *C. papilio* or *C. stygia*" (1886b, p. 458). This 'variety' was raised to species level later as the style was considered too long for either *C. papilio* or *C. stygia* (1888b, p. 43). *C. attenuata* differs in having "narrower and smaller" abdominal segments and style and stylets shorter than *C. gigas* or *C. murchisoni* (1886b, p. 456-457).

Style length is unsuitable as a character for specific differentiation since only when cameo and intaglio are available is it possible to know if the long, needle-like, distal portion of the style is preserved. Furthermore, the style is a hollow structure and appears "relatively broad" simply due to flattening during burial. It is therefore suggested that all the above mentioned 'species' belong to either *C. papilio* or *C.*

stygia, which form the subject of the present preliminary study. An account of the morphology of the species is given elsewhere (Rolfe, in press).

Although Salter (1860, p. 156) stated that *C. stygia* had its "margine ventrali plus minusve angulato," the diagnostic character of *C. papilio* was "the much shorter body — scarcely longer (tail included) than the great carapace — [which] easily distinguishes it." Jones and Woodward (1885, p. 392; 1886a, p. 341; 1888b, p. 36) misrepresented Salter's diagnosis of these two species, thus "as mentioned by Salter, one (*C. papilio*) has the carapace more oblong than the other (*C. stygia*)." This revised diagnosis led them to suggest (1885, p. 393; 1886a, pp. 341-342; 1888b, p. 36) that only the first of the three figures "termed *C. papilio,* evidently from oversight" by Salter (1860, p. 154) was in fact that species, the remaining two being *C. stygia.* Salter had already suggested (1860, p. 156) that there were "at least two varieties of carapace in *C. stygius* itself." Subsequent workers have found it difficult to distinguish the two species, and it has been suggested that they are identical (Størmer, 1935, p. 294). This difficulty was also encountered in the present study and hence the museum collections of material available to Salter and Jones and Woodward (*i.e.* their hypodigm) have been restudied to see if the species distinction could be maintained.

One complicating factor in the use of the older collections is the separation of parts from counterparts. Specimens of identical dimensions occur in different institutions, and without bringing all the material together it is impossible to be certain that part and counterpart of the same individual are not treated as two individuals. This does not affect the present study, however, since it is arguable that such duplication will be distributed evenly throughout the sample.

Two new collections have been examined to determine if, for example, *C. papilio* and *C. stygia* were allopatric or even successional species (= chrono- or palaeospecies). The first of these, the A. Ritchie collection in the Grant Institute of Geology, Edinburgh University, came from the '*Jamoytius* Beds', half a mile up the Logan Water from Logan House (Ritchie, 1960, p. 647). The other was collected by J. S. Jennings from a horizon *ca.* 700 feet higher in the succession at the locality near Logan Reservoir known as Shank's Castle (Peach and Horne, 1899, p. 573). This collection is now deposited in the Geology Department, University College of North Staffordshire.

The older material is housed in the several museums listed on Table 1. Few of the specimens have accurate localities indicated, but the majority probably came from the Shank's Castle region. Several other localities are known, however, and these have been detailed by Etheridge (1873b, p. 49). The authors wish to thank the several curators for access to collections, and Professor H. B. Whittington for reading the manuscript of this paper.

Salter's criterion for distinguishing *C. papilio* from *C. stygia* by the number of segments protruding from the carapace is artificial, since it depends solely on the degree to which the thorax and abdomen are impacted into, or drawn out from the carapace after death or exuviation. Jones and Woodward suggested that "*C. stygia* was rather larger than *C. papilio*; its telson was larger; the carapace was markedly distinct by its trapezoidal outline, deep ventral region, and mucronate antero-dorsal angle, which was not nearly so often lost in fossilization as the front angle of *C. papilio*" (1885, p. 395; 1886a, p. 344; 1888b, p. 40). Style length has already been criticised as a specific character; thus of 202 styles measured only 64 were complete and associated with the last abdominal segment. The ratio of style length/last abdominal segment length ranges from 1.5 to 2.9, and a scatter diagram of this ratio showed normal uncorrelated variation when plotted against the last abdominal segment length. This does not confirm Jones and Woodward's assertion that "in *C. stygia* the style is usually rather more than twice, and in *C. papilio* only about twice as long as the ultimate segment" (1888b, p. 39).

The remaining two characters utilised by Jones and Woodward are carapace size and shape. We here define a 'size factor' P such that

$$P = \log (LH)$$

and a 'shape factor' Q such that

$$Q = \log (L/H)$$

where L and H are the overall length and height of the carapace in millimeters. Figure 1 shows the relationship between the size and shape factors for the 128 intact carapaces listed in Table I. The distribution of points is the same as would have been obtained by plotting L against H on double-log paper and rotating the diagram through 45°. The object of performing the logarithmic transformation and rotation analytically is two-fold: to normalise the distribution of the shape factor Q, and to simplify investigation of the extent to which growth in *Ceratiocaris* is allometric.

The overall mean value of the shape factor and standard deviation were found to be

$$\bar{Q} = 0.2775 \pm 0.05917$$

corresponding to a geometric mean value of the ratio L/H of 1.894. The regression of Q on P was calculated by the first-moment method of Wald and Bartlett. The observed P values were divided into five groups and the mean values of Q and P were found for each group, the number of points in each group being 20, 20, 48, 20, and 20. The five mean points are shown on Figure 1, ($\bar{Q}_1$-$\bar{Q}_5$). Their coordinates are (2.8109, 0.3097), (3.0779, 0.2787), (3.2100, 0.2717), (3.3350, 0.2698), and (3.4830, 0.2646).

The regression is thus non-linear, although as may be seen from Figure 1, the four points $\bar{Q}_2$-$\bar{Q}_5$ lie on a practically straight line. The deviation of $\bar{Q}_1$ from this line is scarcely significant, and the line itself does not depart significantly from a direction parallel to the P axis, if the first group of points is ignored.

If we interpret the assemblage as a growth series, it follows that growth is isometric except in the range of size for which P is less than 3.07 (LH less than 1175 mm.^{2}). In this latter size range, growth is not isometric, though the degree of allometry is small and is barely significant.

Changes in the allometric constant during growth are well known in crustaceans, and commonly separate two distinct instars or mark a more critical ecdysis such as the prepuberty moult (Teissier, 1960; Simpson, Roe, and Lewontin, 1960, pp. 412-415).

If we discard the 20 smallest specimens and test the marginal distribution of the remaining 108 Q values by plotting on probability paper, we find that the distribution is an almost perfect unimodal normal curve (a straight line plot). There is thus no evidence to justify splitting up the assemblage on the basis of carapace shape. If, moreover, we regard the assemblage as a single homogeneous sample of a single species, we can readily calculate confidence limits for Q values, to test whether a given specimen may reasonably be regarded as a member of the assemblage. (It will be as well to withhold judgment in the case of very small specimens, but otherwise there should be no need to worry about allometry.)

The first writer (W.D.I.R.) has been unable to trace either of the syntypes of *C. papilio* (Salter, 1859, p. 262) and hence specimen GSM 7479, the original of Salter's 1860, p. 154, fig. 1, is here treated as the neotype of the species. Jones and Woodward accepted this specimen as a genuine *C. papilio* (= M.P.G. x 1/5 in 1885, p. 393; 1886a, p. 342; 1888b, p. 36). Calcula-

TABLE I

Length (L) and height (H) of 128 museum specimens of ceratiocaridid carapaces from the Lesmahagow area, in millimeters

Specimen number	L	H
GSM-165-2	25	11
BM-24161	26	12
BM-24163	28	13
BM-59648	35	15
BM-16483	33	16
H-no number	28	19
Ke-09 123 fu	34	16
Ke-09 123 cg	42	15
Ke-Airdrie Coll.	34	19
J-LW8 R2	34	19
Ke-09 123 dy	36	18
Ke-09 123 cb	36	19
Ke-R22	37	20
GSE-6650	39	19
Ke-09 123 cd 2	41	19
BM-45161	39	20
J-27	44	18
H-Stark Coll.	45	21
BM-24150	43	23
AR 59-152	43	24

Specimen number	L	H
Ke-09 123 ed	48	22
GSM-X 1/13	41	26
Ke-R29	43	25
J-LW8 Q2	45	25
GSM-256	45	25
AR 59-146	49	23
BM-24151	47	24
Ke-R23	44	26
BM-41895	45	26
BM-24160	45	26
H-A1901	47	26
Ke-09 123 ex	47	26
BM-24158	50	25
AR 59-149	47	27
Ke-R8	53	24
Ke-Airdrie Coll.	48	27
E-1902/30/11	54	25
J-LW8-L	54	25
H-Macnair Coll.	54	25
H-A1902	52	26

Specimen number	L	H
H-66	52	26
AR 59-108	52	26
BM-16495	53	26
Ke-09 123 gb	53	26
BM-24164	52	27
H-A1908	52	27
GSM-7479	57	25
GSE-6647-1	55	26
BM-16501	52	27
K-5-3	49	30
Ke-R28	49	30
BM-24157	57	26
Ke-09 123 dn	50	30
GSM-87338	50	30
AR 59-148	54	28
E-1902/30/9	51	30
K-6-1	48	32
GSE-6647-2	57	27
H-no number	52	30
Ke-09 123 cn	60	26
K-5-2	51	31
J-LW9 E	59	27
Ke-R1	57	28
GSM-272	54	30
H-A1903	56	29
BM-no number	56	29
AR 59-154	58	28
K-5-1	52	32
H-A1904-1	49	34
AR 59-Q	60	28
BM-41896	60	28
Ke-R2	56	30
E-1902/30/7	53	32
H-A1908-3	53	32
BM-16517	57	30
Ke-09 123 dz	58	30
GSM-no number	55	32
H-A1908-2	55	32
H-T.Wise Coll.	58	31
GSM-X 1/22	60	30
Ke-09 123 el	62	30
Ke-R3	62	30
H-A1904-2	55	34
K-8	64	30
Ke-09 123 ey	60	32
E-1902/30/4	52	37
AR 59-153	60	33
AR 59-144	60	34

Specimen number	L	H
AR 59-106	57	36
K-6-2	57	36
E-1902/30/10	71	29
E-1902/30/1	69	30
K-1	56	37
BM-16513	56	37
Ke-R33	62	34
AR 59-M	68	31
K-7	65	33
AR 59-P	67	32
BM-41894	64	34
J-LW8 B	59	37
H-A1900-1	58	38
Ke-R4	69	32
BM-16482-1	67	33
BM-16482-2	62	36
H-A1900-2	66	34
Ke-09 123 ez	74	33
BM-24153	67	37
AR 59-147	66	38

Specimen number	L	H
BM-24155	72	35
Ke-R9	78	33
AR 59-150	63	41
AR 59-151	70	38
BM-58669	83	33
Ke-R25	66	42
BM-24149	73	39
E-1891/92/6	80	36
Ke-09 123 ea	68	43
Ke-R24	70	43
BM-41898	83	37
K-3	75	41
BM-16479	82	42
GSM-X 1/21	85	46
E-1865/11/17	74	53
Ke-09 123 ce	84	47
BM-45154	90	47
GSM-X 1/19	105	50
Ke-09 123 dr	96	61
H-Macnair Coll.	100	70

Ranked according to increasing size factor P = log (LH); the five groups delineated by the heavy lines are those referred to in the text.

Repositories: AR 59 - Ritchie Collection, Grant Institute of Geology, Edinburgh University; BM - British Museum (Natural History), London; E - Royal Scottish Museum, Edinburgh; GSE - H. M. Geological Survey, Edinburgh; GSM - H. M. Geological Survey Museum, London; H - Hunterian Museum, Glasgow University; J - Jennings Collection, Geology Department, University College of North Staffordshire; K - Kilmarnock Public Museum; Ke - Kelvingrove Museum, Glasgow.

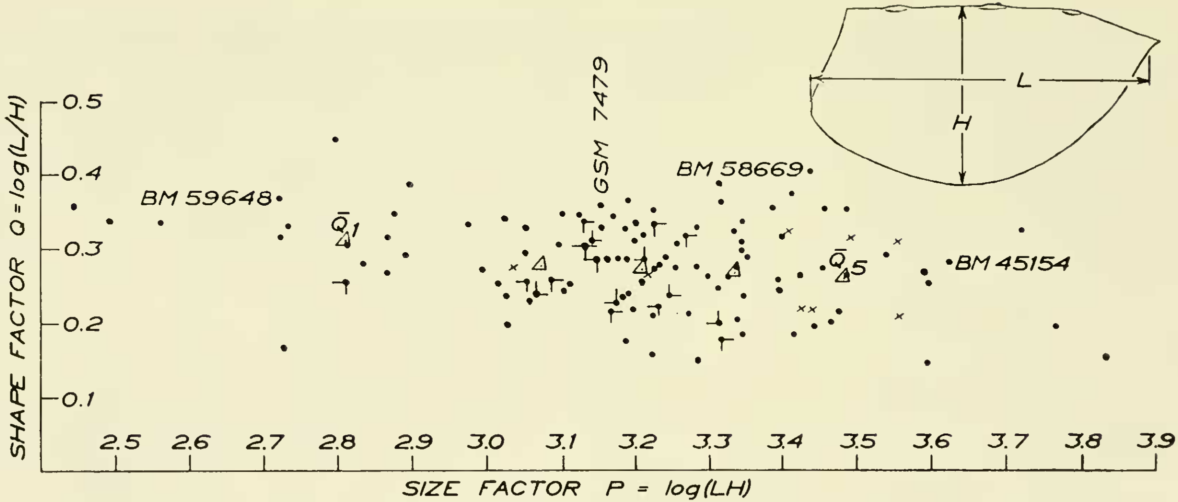

Fig. 1. Scatter diagram of the relationship between shape and size factors for carapaces of *Ceratiocaris papilio* Salter. Dots indicate 128 Lesmahagow specimens and ticks show number of individuals of identical dimensions. Crosses indicate eight specimens from the neighbouring Hagshaw Hills inlier, inserted for comparison but not included in the calculation of the five mean values $\bar{Q}_1 - \bar{Q}_5$ marked by points within triangles. Dots labelled are: GSM 7479 — suggested neotype of *C. papilio* Salter (Geological Survey Museum, London); BM 58669 — 'abnormal' specimen of *C. papilio* figured by Jones and Woodward, 1885, pl. 10, fig. 1, etc., (this and following specimens in British Museum, Natural History); BM 45154 — "*C. stygia*" figured by Jones and Woodward, 1885, pl. 10, fig. 2, etc.; BM 59648 — specimen identified as *C. inornata* by Jones and Woodward. Diagram at upper right shows outline of right carapace valve with dimensions used in defining shape and size.

tion shows that this specimen lies within the 95 percent confidence limits for group 3. The 'primary' types of *C. stygia* are unknown but one of the "good specimens of *C. stygia*" figured by Jones and Woodward (1885, pl. 10, fig. 2; 1888b, pl. 12, fig. 2) BM 45154, is similarly within the 95 percent confidence limits for group 5. *C. stygia* is thus not separable from *C. papilio* on statistical or indeed any other present evidence, and the former junior synonym should be suppressed. The morphospecies *C. papilio* and *C. stygia* form the one biospecies (or transient species) *C. papilio*. It is worth noting that the specimen of *C. papilio* figured by Jones and Woodward (1885, pl. 10, fig. 1; 1888b, pl. 12, fig. 1) BM 58669 is 'abnormal,' as can be seen from its position on Figure 1.

No significant differences in P or Q can be detected in the stratigraphically separated material of the Ritchie and Jennings collections.

There is a notable lack of clustering in terms of the size factor P corresponding to the mean size of successive moult stages or instars. Attempts to divide the Ritchie or Jennings specimens alone into instars were also unsuccessful. Intra-instar variation may obscure the limits of successive instars if sufficiently great, but not all crustaceans obey Brooks' Law (Needham, 1950, pp. 10-11), and *C. papilio* may be another exception. At least part of this difficulty is due to sampling and preservation. Thus small individuals are only rarely collected (see Fig. 1) and all large individuals found have been incomplete. Relatively gigantic specimens up to two feet in total length occur both in the Lesmahagow and Hagshaw Hills inliers, but they can only be reconstructed from fragments and hence do not appear on Figure 1. A further complicating feature of the few large specimens available is their distinctive dendritic carapace ornament. It can be argued, however, that this ornament is characteristic of adult instars (Rolfe, in press). Such giant individuals must have had younger growth stages coincident in size with the specimens of Figure 1, and no such dendritic ornament has been observed in that size range. It seems preferable to extend the name *C. papilio* to include these large individuals, at the risk of 'lumping,' until better sampling has been made.

SUMMARY

Of ten species of *Ceratiocaris* recorded from the Lesmahagow inlier, only *C. papilio* and *C. stygia* are sufficiently well founded to demand preliminary investigation. Both Salter's diagnosis of these two species and Jones and Woodward's subsequent definitions are artificial. Analysis of 128 carapaces in museum collections shows that *C. papilio* is indistinguishable from *C. stygia*, and the latter should be suppressed as a junior synonym.

Carapaces of *C. papilio* show isometric growth except in the smallest individuals. The material cannot be resolved into a series of distinct instars.

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